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DISCONTINUOUS VARIATION AND THE ORIGIN OF SPECIES*

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That distinct and separate qualities expressed in recognizable external characters may appear suddenly, or disappear completely, in a series of generations of plants, has been a matter of common observation so long that it would be difficult to hunt out and fix upon the first instance of record.

The significance of such phenomena was obviously beyond the comprehension of the earlier botanists and it is evident that a rational recognition of the phylogenetic value of sports and anomalies necessarily awaited the development and realization of the conceptions of unit-characters of the minute structures which are the ultimate bearers of heredity, and of the inter-dependence of the two in such manner as to constitute actual entities as embodied in Darwin's pangenesis, de Vries' intra-cellular pangenesis and in Mendel's investigations upon heredity. It is equally apparent that a proper interpretation of the facts in question, and their distinction from the results of hybridization was possible only by means of the analysis of the collated results of observations upon series of securely guarded pedigree-cultures, in which the derivation of all of the individuals of several successive generations had been noted. For it is now thoroughly realized that the main questions of descent and heredity and of evolution in general are essentially physiological, and as such their solution is to be sought in experiences with living organisms and not by deductions from illusory "prima facie" evidence, which has been so much in vogue in evolutionary polemics, nor

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by " interpretations of the face of nature " with the accompanying inexact methods and superficial considerations. It was upon the safe basis of the first-named conceptions, and by means of the methods entailed that de Vries has so successfully grappled with the problems involved in the investigation of the part played by discontinuous variation in evolution.

In view of the amount of orderly and well-authenticated evidence now at hand, it may be assumed as demonstrated that characters and groups of characters of appreciable physiological value, originate, appear in new combinations, or become latent, in hereditary series of organisms in such manner as to constitute distinct breaks in descent.

This is the main thesis of the mutation theory: the saltatory movements of characters, regardless of the taxonomic value of the resultant forms. That the derivatives might be considered as species by one systematist, and varieties by another is quite incidental and of very little importance. The main contention lies in the claim that characters of a definite nature appear, and become inactive suddenly, and do not always need thousands of years for their infinitely slow external realization, or for their gradual disappearance from a strain.

Of course the principal corollary of the mutation-theory is that the saltations in question do result in the constitution of new species and varieties. As a matter of interest it may be stated that all of the systematists who have seriously examined the adult mutants of the evening-primroses cultivated in the New York Botanical Garden have held the opinion that certain ones were to be considered as species and others as varieties.

Furthermore, these conclusions are confirmed when the characters of the mutants are subjected to statistical methods of investigation. In the observations of Dr. Shull, which will be presented more fully before the Botanical Society of America, it has been found that qualities of the mutants, susceptible of measurement, depart definitely and clearly from the parental type and fluctuate about a new mean, and do not intergrade with the parental form. The amplitude of fluctuation about the new center is greater than that of correspondent parental qualities,

and the degree of correlation is much less in the mutants than in the parent. This is seen by inspection to be true in one species during the first year of its existence, and is confirmed by the exact observations on other forms a dozen years after their mutative origin. Consequently the features in question may not be taken to be in any way the result of selection but are in themselves new qualities.

Lamarck's evening-primrose offers such striking and easily recognizable examples of discontinuous variation, and has been the object of so much detailed study that we are in danger of giving way to the supposition that the mutation-theory rests upon the facts obtained from this plant alone. It is to be said, however, that if it and all of its derivatives were destroyed, the results of experimental studies which have been made upon mutations in other species, upon the behavior of retrograde and ever-sporting varieties, the occurrence of systematic atavism, and of taxonomic anomalies, pelories and other morphological features would furnish ample support for the conception of unit-characters, and serve to establish the fact that mutations have occurred in a number of species representing diverse groups.

It is now becoming plainly apparent that the phenomena of hybridization, by the opportunities afforded for the study of the included unit-characters in a segregated condition, for the analysis of complex characters, and of the various principles governing the transmission, activity, dominancy, latency and recessivity of characters, promise to yield results of the first magnitude concerning the mechanism of descent and heredity. The possibilities of crosses between species comparatively widely different in morphological and physiological constitution among plants indicate that the ultimate generalizations upon hybridism will find broader exemplification in plants than in animals.

It is pertinent to point out in this connection that the unguarded use of the terms "variation" and "mutation" to designate phenomena of segregation and alternative inheritance when races or species are thrown together in a hybrid strain is bound to result in much confusion, especially in dealing with plants, since it is well known that direct mutants of either parent occasionally occur in such mixed strains.

From this last consideration we pass naturally to a discussion of the nature of the material which may be of use in the study of fluctuating and discontinuous variability. It needs no argument to support the assertion that a successful experimental analysis of the behavior of separate characters may be carried out only when dealing with series of organisms fluctuating about a known mean with a measurable amplitude of variability.

Systematic species as ordinarily accepted generally consist of more than one independent and constant sub-species, or elementary species which may not be assumed to interbreed or intergrade, unless actually demonstrated to do so by pedigreed cultures. So far, but few elementary species have been found to interbreed. A due recognition of this simple fact would save us a vast amount of pyramidal logic resting on an inverted apex of supposition.

Again the accumulation of observations upon the prevalence and effect of self- and cross-fertilization has totally unsettled the generalizations current within the last few decades. Briefly stated, a moderate proportion of the flora of any region is autogamous, a large proportion both autogamous and heterogamous, and a moderate proportion entirely heterogamous. The relative number of species included in the categories indicated varies greatly in different regions. To assert the deleterious effects of self-fertilization, of all or a majority of plants, is to base a statement upon evidence that lacks authentication and correlation, as has been strikingly demonstrated by recent results. As a matter of fact no phase of evolutionary science is as badly in need of investigation as that which concerns the effects of close and cross-breeding.

It is also to be said that current misconceptions as to the extreme range of fluctuating variability of many native species have arisen from a failure to recognize the composite nature of the Linnaean, or group-species, upon which observations have been based, as I have found with the common evening-primrose.

The demands of ordinary floristic work are usually met by the formulation of collective species, which are in fact, an undeniable convenience, and necessity perhaps, for the elementary teacher and

the amateur. Upon the specialist in any subject rests the obligation to furnish his non-technically trained constituency with conceptions of the facts and principles within the domain of his investigations, which will be inclusive, and easy of comprehension. But if in accordance with this requirement, the systematist contents himself with this looser, and with due regard it may be said, more superficial treatment, and does not delineate clearly the elementary constituents of a flora, or falters in carrying his analysis of relationships to its logical end, he fails notably in the more serious purpose of his investigations, and his work must be supplemented and extended before it becomes an actual basic contribution to the physiologic or phylogenetic branches of the science. To study the behavior of characters we must have them in their simplest combinations. To investigate the origin and activity of species we must have them singly and uncomplicated.

Lastly, we may turn to a phase of the subject which has, as yet, received nothing but speculative consideration — that of the causes which induce the organization of new characters and which stimulate their external appearance. The recurrence of the known mutants of Lamarck's evening-primrose, and the occurrence of new mutants of other species has taken place in New York and Amsterdam under conditions that lead to the definite conclusion that a favorable environment including the most advantageous conditions for vegetative development and seed-production facilitates the activation and appearance of latent qualities; and the inference lies near at hand that such conditions also facilitate the original organization of new unit-characters or changes in these entities. We conclude therefore that favorable environment promotes the formation of new species as suggested by Korshinsky, and that new species do not arise under the stress of infra-optimal intensities of external factors as proposed by Darwin.

Furthermore it has been found that certain qualities arise and disappear more numerously, and presumably more readily than others in a mutating strain. Thus, those embodied in the mutants *Onagra* (*Oenothera*) *oblonga*, and *nanella* find external reali-

zation in many more individuals than those which constitute the differentiating features in *rubrinervis*, *scintillans*, *gigas*, *elliptica*, *subovata*, and others.

Again the inspection of the cultures made in Amsterdam and New York demonstrates that the last-named locality offers more favorable soil and climate for the evening-primroses. Correlated with this I am able to report that careful attention to the cultures has resulted in an increase of the proportion of mutants from the five per cent. maximum of de Vries to more than six per cent. in the last season, in the American cultures, and to say that some forms which did not reach maturity, and others which did not occur, in Amsterdam, may find in New York a climate in which they carry out their entire development. The cultures of Lamarck's evening-primrose now being carried on include 14 recognizable mutants, and it is pertinent to state that I have mutants of other species which will be duly described after they have completed a cycle of development.

All components of the environment may not be taken to be of equal value in the induction of new qualities, and I by no means wish to give the impression that the problem is on the point of being solved, but our hopes have been raised to the highest pitch that we may soon be able to discern the factors more or less directly concerned.

To be able to bring the causes operative in the formation and structural expression of qualities, that is, the moving forces of evolution, within the range of experimental investigation would be a triumph worthy the best effort of the naturalist; in that it would give us the power to give new positions to qualities and thus produce new organisms, its importance would rank well with that of any biological achievement of the last half century.

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A PASPALUM NEW TO THE WEST INDIES

By George V. Nash

In working over some grass material secured by Mr. A. H. Curtiss (no. 379) on the Isle of Pines, just to the south of Cuba,